# ALTERNATIVE DIGITAL SCANSOR DESIGN IN THE NEW CALEDONIAN GEKKONID GENERA *BAVAYIA* AND *EURYDACTYLODES*

### AARON M. BAUER AND ANTHONY P. RUSSELL

Gekkonid feet are complex and highly integrated functional units. Convergence and parallelism are common themes in gecko digital design. Alternatively, closely related geckos may exhibit widely differing toe morphologies within a framework of phylogenetic constraint.

The New Caledonian carphodactyline geckos *Bavayia* and *Eurydactylodes* are closely related to one another yet they exhibit marked differences in external digital form. *Bavayia* possesses divided scansors and a highly arcuate penultimate phalanx. In *Eurydactylodes* the scansors are undivided and the penultimate phalanx is not raised. Internally *Bavayia* has a divided vascular sinus and a region of adipose tissue which helps to distribute forces laterally in conjunction with the divided pad. Proximally the digits of *Bavayia* are filled with adipose tissue which provides passive support and conformation for the non-scansorial friction pads. In *Eurydactylodes* a huge vascular sinus transduces forces directly from the penultimate phalanx.

Differences in scansor morphology between the taxa are related to the differences in control mechanisms of single versus divided pads. The functional significance of the alternative scansor designs is unclear, but the divided scansors of *Bavayia* may have played a role in the relative success of the genus in New Caledonia. □ *Gekkonidae, Carphodactylinae, Bavayia, Eurydactylodes, digits, scansors, functional morphology, evolutionary constraint.*

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The scansors of the gekkonid foot are extremely complex and highly integrated functional units (Dellit, 1934; Russell, 1972, 1975, 1976, 1979, 1981, 1986). The adhesive ability of geckos is dependent not only upon the setal microstructures that interact with the substrate (Hiller, 1968, 1969, 1975), but also upon internal features of the scansors that transmit forces to the seta-bearing surfaces (Russell, 1975, 1981) and permit the distribution of forces associated with weight-bearing (Russell, 1986).

The precise nature of the organisation of components of the musculo-skeletal and circulatory systems, as well as connective and adipose tissues varies among the taxa studied to date. Distantly related taxa, however, often cope with similar locomotory demands (frequently substrate related) in near identical fashion. This has been well-documented in the case of ecologically equivalent members of the subfamilies Gekkoninae and Diplodactylinae (Russell, 1979) and has even resulted in parallel radiations of geckos in these groups on the basis of key innovations (sensu Liem and Osse, 1975) in pedal structure and scansor architecture. Within a single subfamily, similar convergences have also been noted in genera occupying similar spatial niches or exploiting particular substrates (e.g. Russell, 1976). Indeed, a particular morphology, such as that characterising 'leaf-toed' geckos, may have been independently derived in many lineages (Russell and Bauer, 1989).
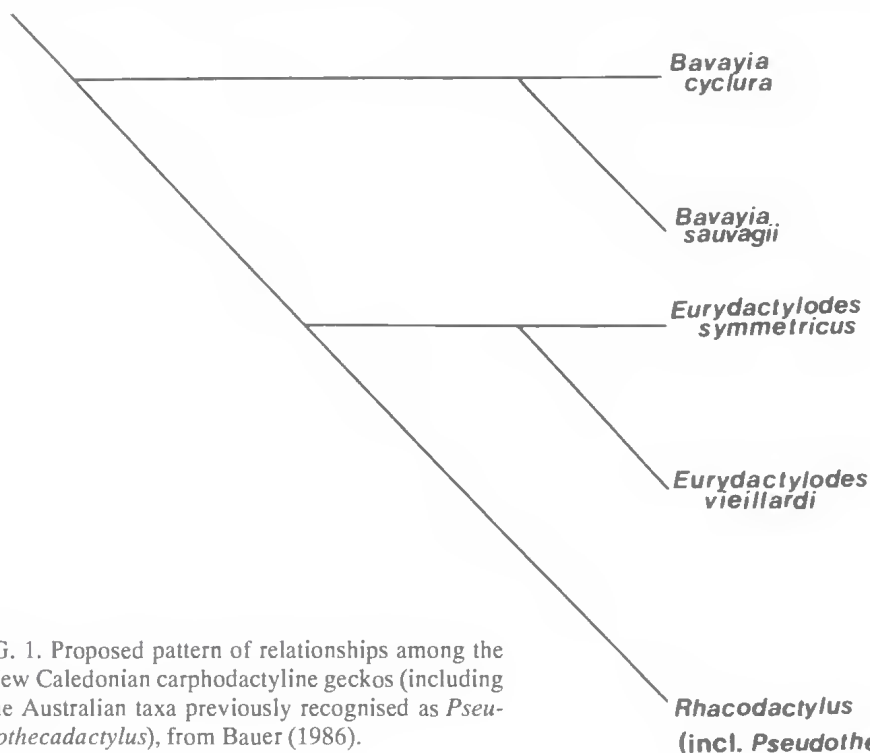
Conversely, even closely related taxa may exhibit a diversity of digital forms within the constraints of shared descent (see Brundin, 1968). Russell (1976), for example, demonstrated a morphotypic series in digital design and complexity in the gekkonine genera *Pachydactylus* and *Hemidactylus*. Both of these genera are speciose and ecologically diverse and exhibit variations in both external and internal digital design.

The subfamily Diplodactylinae is less speciose than the Gekkoninae and much more geographically circumscribed, with all taxa occurring in the Southwest Pacific (Australia, New Zealand and New Caledonia). None the less, there is great ecological diversity in the group, which includes burrowers, terrestrial forms and arboreal species. Like marsupials, the diplodactylines represent an ancient independent lineage which includes major radiations to some extent comparable to those of their more widespread relatives.

The parallels between the Diplodactylinae and Gekkoninae are striking (Russell, 1979) but the analysis of the diplodactyline radiations is interesting in its own right. Unfortunately, few studies have examined diplodactyline morphology to date. Russell (1972, 1979) examined the pedal morphology of several species in the Diplodactylinae, but his data were derived almost exclusively from gross dissection. Further, Russell lacked an explicit hypothesis of relationship among the diplodactylines upon which he could interpret the observed anatomy. Such an hypothesis is essential if the evolutionary and ecological significance of morphologies are to be evaluated in a phylogenetic context (Lauder, 1981, 1982).

In this paper we examine aspects of digital scansor morphology in representatives of the New Caledonian genera *Bavayia* and *Eurydactylodes*, two closely related diplodactyline geckos in the tribe Carphodactylini. Although Underwood (1954) initially placed the two genera in different subfamilies, he later (Underwood, 1955) reconsidered the affinities of *Eurydactylodes* and placed both genera in his Diplodactylinae. Kluge (1965, 1967) accepted the affinities of these taxa and their close relationship to a third New Caledonian genus, *Rhacodactylus* and included all three in the tribe Carphodactylini. Bauer (1986), on the basis of a morphologically- based cladistic analysis, proposed a specific pattern of relationships among these three taxa (Fig. 1). Although a characteristic previously thought to be diagnostic of the Gekkoninae (sensu Kluge, 1987), the presence of extracranial endolymphatic calcium deposits, has since been identified in *Eurydactylodes* (Bauer, 1989), the overwhelming evidence of other characters suggests that the New Caledonian endemic geckos are indeed closely related. Despite this affinity, the external digital morphology of *Bavayia* and *Eurydactylodes* is markedly different. *Bavayia* is characterised by divided scansors and highly arcuate distal phalanges while the latter possesses single



FIG. 1. Proposed pattern of relationships among the New Caledonian carphodactyline geckos (including the Australian taxa previously recognised as *Pseudothecadactylus*), from Bauer (1986).

subdigital plates and a less markedly raised penultimate phalanx. Outward variation of this nature in the Gekkoninae is generally indicative of major design differences in internal anatomy and consequent functional differences (see Russell, 1972, 1976, 1979). We here assess the specific anatomical differences exhibited by *Bavayia* and *Eurydactylodes* and evaluate significance (if any) of alternative digital designs within the well circumscribed New Caledonian carphodactyline lineage.

## MATERIALS AND METHODS

Specimens examined in this study were collected by the senior author in New Caledonia under the authority of the Service des Eaux et Forêts and have been deposited in the California Academy of Sciences (CAS). In addition, specimens were also examined in the collections of several museums, most notably, the Australian Museum (AMS), the Naturhistorisches Museum Basel (NHMB), the Zoologisches Forschungsinstitut und Museum Alexander Koenig (ZFMK), and the British Museum (Natural History) (BMNH).

Gross external observations and dissections were carried out on formalin-fixed, alcohol preserved museum specimens of *Bavayia* and *Eurydactylodes*. Radiographs of selected specimens were prepared using a self-contained x-ray unit.

Cleared-and-stained preparations were made following a modification of the protocol of Wassersug (1976). Specimens for light microscopy were decalcified, dehydrated, cleared and embedded in paraffin. Sections were cut on a rotary microtome at thicknesses of 8–12μm and stained according to the protocol for Mallory's azan trichrome stain (Humason, 1979). Photomicrographs were prepared with a Wild compound microscope with 35 mm photo attachment. Specimens for scanning electron microscopy were dehydrated through a graded alcohol series, critical point dried and sputter-coated to a thickness of 30nm with gold-palladium alloy before examination with an ISI-DS 130 microscope.

## RESULTS

### EXTERNAL ANATOMY OF THE DIGITS
*Eurydactylodes*
The digits of *Eurydactylodes symmetricus* and *E. vieillardi* are essentially identical in form. The following description is based primarily upon specimens of the latter taxon. The digits are short and broadly dilated. Small fleshy webs are present between digits II and III and III and IV. The penultimate phalanges of digits II -V are mostly subsumed within their respective pads and the claw is carried only a short distance beyond the distal margin of the scansors. The ungual phalanx is firmly connected to the dorsum of the pad by a fleshy sheath. Digits II -V of the manus fan out broadly whereas the first four of the pes are bound together at the level of the metatarsals, restricting the spread of the digits.

The ventral surface of the pads of digits II - IV bear a series of broad scansorial plates that are generally straight proximally and somewhat chevron-shaped distally (Fig. 2A). Proximally, the scansors grade into enlarged subdigital scales that terminate at the level of the proximal portion of the first phalanx and are replaced by small non-setose scales similar to those of the palms. The proximalmost plates are generally non-scansorial (sensu Russell, 1975) but do bear setae. There are typically 10 - 12 expanded plates under the fourth (longest) toe in both species.

Digit one is small and bears a series of about five small friction pads proximal to the minute claw. The claw itself is sheathed and is bordered both laterally and medially by small terminal plates. Unlike all other New Caledonian and New Zealand carphodactylines (Bauer, 1986) these plates are completely separated from one another. The medial plate is substantially larger than the lateral (Fig. 2D).

*Bavayia*
The digits of *Bavayia cyclura* are moderately elongate and broadly dilated distally. As in *Eurydactylodes* the claws of digits II - V extend beyond their respective pads, but are firmly anchored to them by cutaneous sheaths. The penultimate phalanx is very strongly arcuate and rises well above the plantar surface of the pad. Small webs connect the bases of digits II and III, III and IV and IV and V. As in all New Caledonian and New Zealand carphodactylines, metatarsals of digits I - IV are joined, reducing the digital spread of the pes (Fig. 3).

All enlarged subdigital plates except the distalmost are divided and the pairs are strongly angled so that the medial ends meet at the midline far proximal to the lateral termini (Fig. 2B). At about the level of the antepenultimate phalanx the more distal true scansors (defined on their internal morphology - see below) give way to
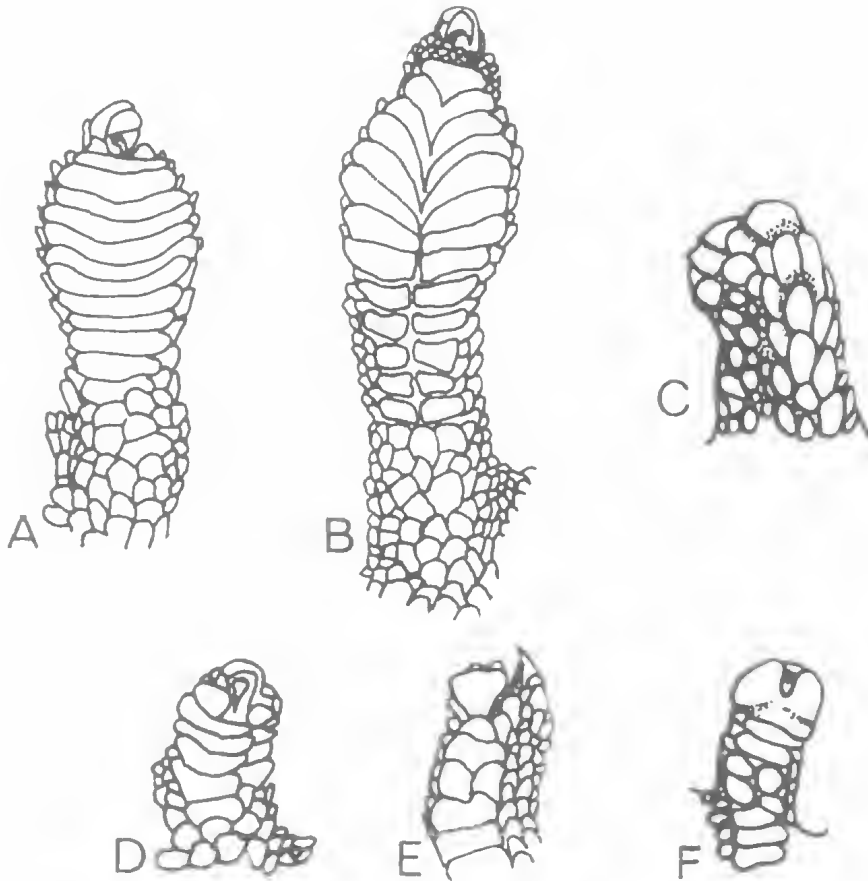
FIG. 2.A. *Eurydactylodes vieillardi* (BMNH 1926.9.17.7), digit III, right pes. B. *Bavayia sauvagii* (BMNH 1926.9 17.25), digit IV, left pes. C. *Bavayia sauvagii* (CAS 159532), digit I, right pes, dorsal view. D. *Eurydactylodes vieillardi* (BMNH 1926.9.17.7), digit I, right pes. E. *Bavayia sauvagii* (BMNH 1926.9.17.25), digit I, left pes. F. *Bavayia cyclura* (CAS 159550), digit I, right pes. Note the architecture of the subdigital plates in A and B and the disposition of the terminal plates in D - F.

simple friction pads. At the metapodial/phalangeal joints the friction pads grade into irregular smaller scales which, in turn, grade into the palmar scales.

Digit 1 of both manus and pes is reduced and carries a series of undivided friction plates, but no expanded pad. In contrast to those of the remaining digits, the claw of digit 1 is minute. It is bordered by a large, cleft terminal plate which is asymmetrical, bearing a larger medial pad (Fig. 2F). A diastema separates the terminal plates from the basal friction plates, which extend well onto the palmar surface.

The digits of *Bavayia sauvagii* are similar in most respects to those of their congeners but are somewhat more elongate and less broad. The scansor pairs of digits II - V are separated by a somewhat broader gap than are those of *B. cyclura* and break up into small scales somewhat more distally. Digital setae are longest at the free margins of the lamellae and appear to be better developed on the true scansors than on the friction plates (Fig. 4). Most notably, the terminal plate of digit I is entirely medial to the claw (Fig. 2E). In dorsal view the claw of this digit appears completely sheathed (Fig. 2C).

INTERNAL ANATOMY OF THE DIGITS
*Eurydactylodes*

The musculo-skeletal system of *Eurydactylodes* and *Bavayia* are essentially identical to that described by Russell (1972, 1979) for the

FIG. 3. Ventral view of the left pes of *Bavayia sauvagii* (CAS 159532) showing the metatarsal binding of the first four digits. Scale bar = 1mm.
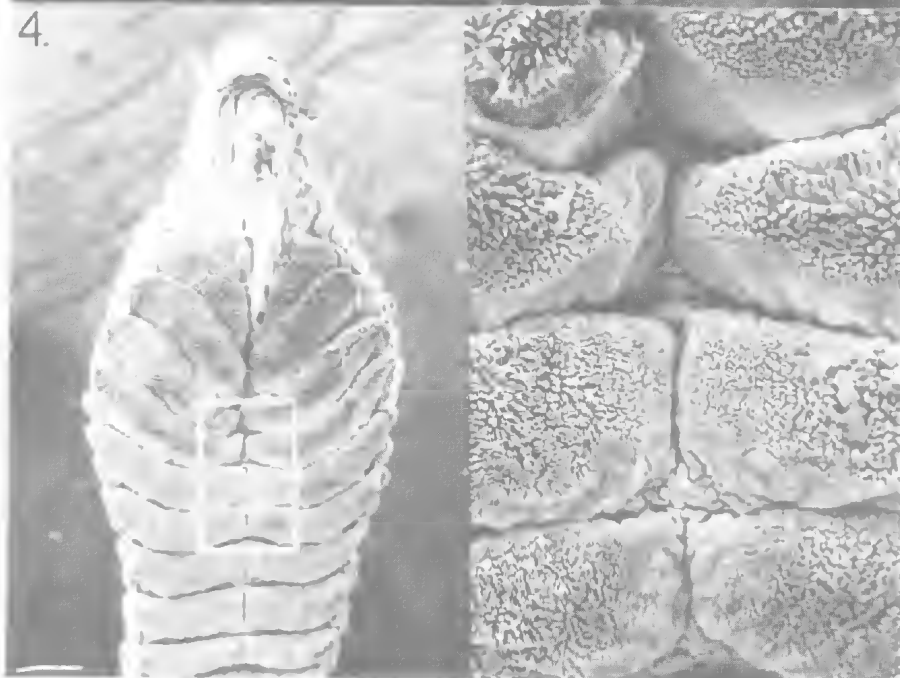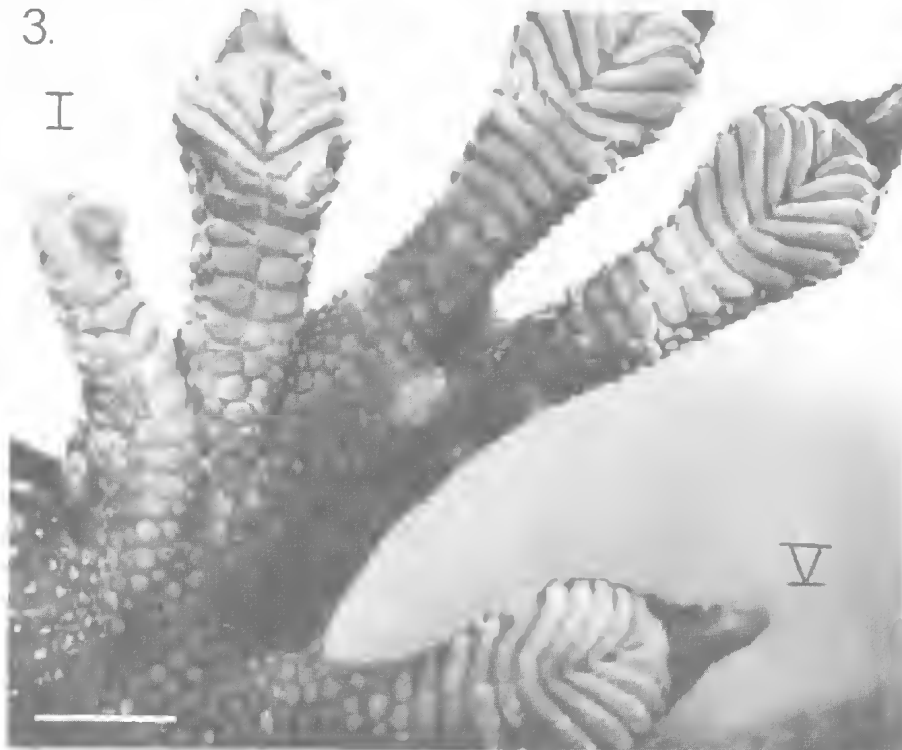


FIG. 4. Scanning electron micrograph of digit IV, right pes of *Bavayia cyclura* (no catalogue number) illustrating the median scansor cleft and the relative decrease in the depth of setal pile near the midline of the toe. Scale bar = 300μm (right side shows 5 X enlargement of box on left).
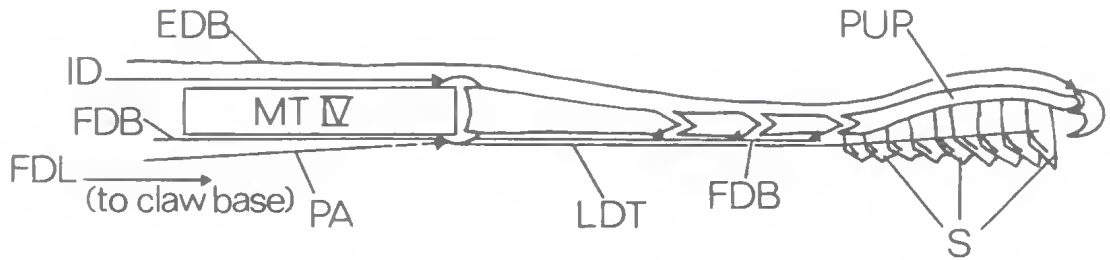
FIG. 5. Diagrammatic representation of the musculo-tendinous system of digit IV of a generalised New Caledonian carphodactyline gecko. EDB = extensor digitorum brevis, FDB = flexor digitorum brevis, FDL = flexor digitorum longus, ID = interossei dorsales, LDT = lateral digital tendon, MT IV = fourth metatarsal, PA = plantar aponeurosis, PUP = penultimate phalanx, S = scansors. Arrows indicate points of attachment of muscles and tendons.

closely related genus *Rhacodactylus*. The phalangeal formulae are unreduced (2-3- 4-5-3 manus, 2-3-4-5-4 pes). The penultimate phalanx is cylindrical in section and arches over the broadest part of the pad. The first phalanx is gcncrally also cylindrical. Intermediate phalanges are strongly depressed and barbell-shaped, with broad epiphyseal surfaces.

The dorsal extensor musculature consists of two asymmetrically developcd bellies for each digit. Each pair of bellies sends a tendon to thc middorsal region of its respective ungual phalanx. The dorsal interossei muscles reach only the lcvel of the metapodial elements and do not send out tendons to thc phalanges. Ventrally, lateral digital tendons extend from the metapodial- phalangeal joint capsule to the proximal borders of each of the true scansors. Digital flexor muscles run in parallel with the lateral digital tendons and insert on the distal cnds of thc phalanges (except the ungual and penultimate phalanges; the long flexor muscle inserts on thc lower part of the base of the ungual phalanx). In addition, the base of the digits receive slips from the femorotibial gastrocnemius (see Fig. 5 for a diagrammatic summary of the muscular and tendinous components of the digit).

Internally, the scansor-bcaring digits (II - V) of *Eurydactylodes vieillardi* are typified by thc presence of an extensive digital sinus systcm consisting of a large central sinus and a reticular network (Figs. 6, 7) supplying both the medial and lateral portions of the scansors with vascularization in association with scansorial control (see Russell, 1981). True scansors are present bencath the penultimate phalanx as well as the more proximal phalanges. There is a minimal amount of loose connective tissuc in the toc, and no adipose deposits wcre evident in histological sections.

*Bavayia*

The external differences between *Bavayia cyclura* and *B. sauvagii* are not manifested in the internal structure of the digits. In both taxa the proximal portion of the digit is largely filled with connective tissue invested with adipose cells (Fig. 8). This condition extends as far distally as the level of the penultimate phalanx whcre true scansors are located. In the region of the scansors lies a central blood sinus which has two lateral chambers, one on either side of the midline scansor cleft (Fig. 9). In all areas of the toe connective tissue, usually containing adipose deposits, occupies the dorsal portion of the pad and the lateral portions of the scansorial plates themsclves.

## DISCUSSION

PHYLOGENETIC CONSTRAINTS

The observable morphologies of living organisms arc strongly influenced by the history of thc taxa that possess them (Lauder, 1982). The influcncc of past environmental factors on form and function of organ systems should thus be reflected in dcscendent taxa, and taxa with shared descent should exhibit certain such historical features, or constraints, in common.

*Eurydactylodes* and *Bavayia* appear to share a number of digital features as a result of common descent. In common with *Rhacodactylus* (including *Pseudothecadactylus*), *Hoplodactylus* and *Naultinus*, metatarsals 1 - IV, espccially III and IV are parallel to one another, thus reducing digital spread (Russell, 1972; Bauer, 1986). These genera also share a 'simplified' muscular system in which the distal phalanges are free of thc fleshy portions of the flexor and extensor muscles. Likewise, the digits receive no dircct

FIG. 6. Cross-section through the fourth digit, right pes of *Eurydactylodes vieillardi* (ZFMK 16113) under the anterior portion of the penultimate phalanx. Note the many vascular lacunae (marked with X's) that are components of the reticular network of vessels that regulates and transduces pressure within the scansors. Abbreviations as in Figure 5. Scale bar = 250μm.
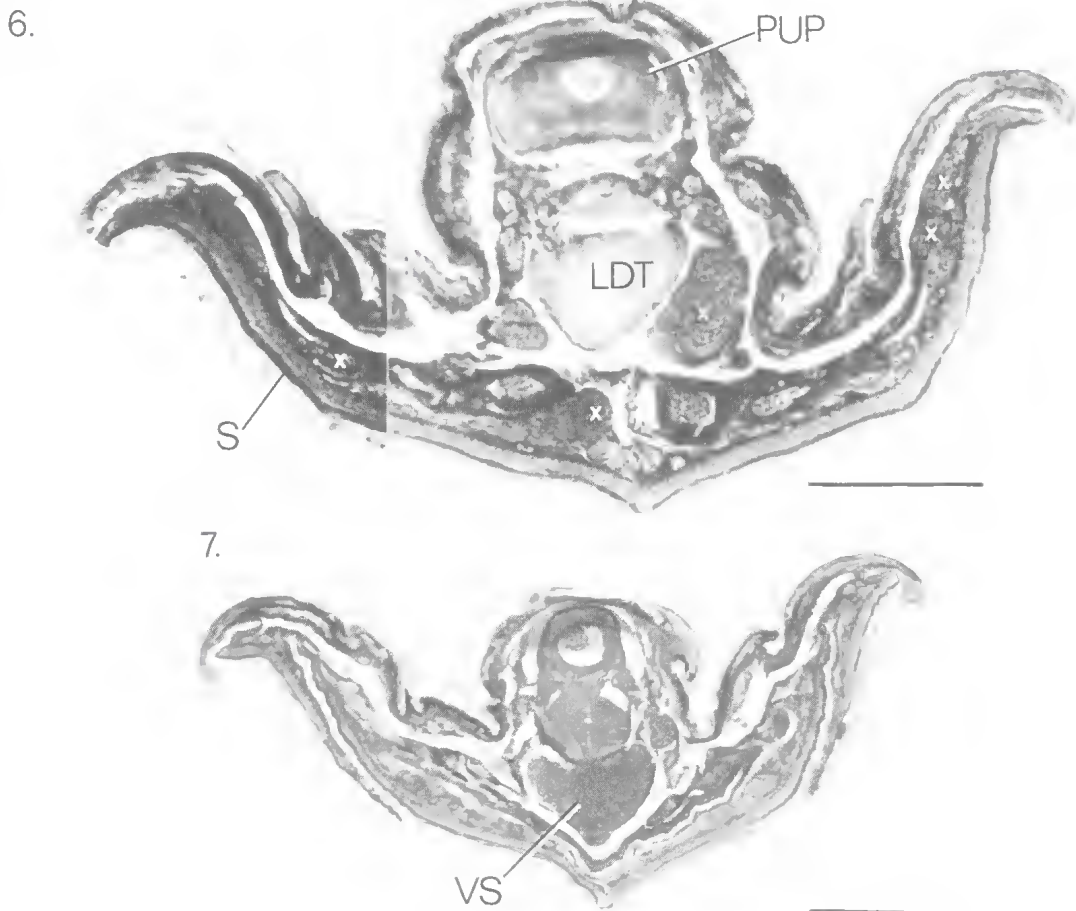


FIG. 7. Cross-section slightly proximal to Figure 6 showing the large central vascular sinus (VS) typical of *Eurydactylodes*. Note the absence of adipose tissue. Scale bar = 250μm.

tendinous slips from the dorsal interossei muscles. The presence of small, asymmetrical terminal plates on digit I is also a synapomorphy of the padded genera of carphodactylines (Bauer, 1986). At a more restrictive level, that of the broader padded carphodactylines, *Bavayia* and *Eurydactylodes* share the extreme flattening of intermediate phalanges.

ALTERNATIVE DESIGNS

The major differences in the digital morphology of *Bavayia* and *Eurydactylodes* are directly related to the scansors themselves, namely exter-

nal scansor form and the internal support system of the scansors and friction pads. The autapomorphic condition of the completely divided apical plates of *Eurydactylodes* (Fig. 2D) seems unlikely to be of functional significance.

Russell (1979) associated scansor division with the dissociation of the penultimate phalanx from the pad of the toe. In gekkonines scansor division is associated with the division of the blood sinus into two large lateral branches (Dellit, 1934; Russell, 1976, 1979), ensuring intimate contact despite the lessening of the direct pres-

sure link through the penultimate phalanx. Russell and Bauer (1988) have demonstrated that this pattern is also generally associated with the inception of some sort of paraphalangeal support for the lateral regions of the pad, probably associated with the transmission of force to the sinus in the absence of a direct phalangeal transmission system. Scansors directly beneath the midline are subsequently lost with the absence of an effective scansor control mechanism in that region. The highly arcuate penultimate phalanx of *Bavayia* spp. seems to function to some degree in this manner, although here the sinus is only truly divided dorsal to the distalmost scansors. More proximally the central sinus sends two subdivisions out to the scansor pairs (Fig. 9). Although somewhat free of the pad, the penultimate phalanges of *Bavayia* are much less independent than in some gekkonines such as *Gehyra. Eurydactylodes*, on the other hand, with its undivided scansors possesses an undivided central sinus and the penultimate phalanx, although arcuate, is not strongly so.

In addition to the subdivision of the scansors the two genera also differ in the distribution of adipose tissue in the digit and the extent of the vascular network. In *Eurydactylodes* there is very little adipose tissue, and the posterior expansion of large blood lacunae is suggestive of a posterior extension of the scansors (sensu Russell, 1975). In *Bavayia*, on the other hand, the scansors are limited to the area under the penultimate phalanx and the remainder of the expanded plates are filled with adipose tissue as is the entire dorsal surface of the toe. A subdigital adipose zone has been reported in the other New Caledonian genus, *Rhacodactylus* (Russell, 1972, 1979; Bauer, 1986) where it runs in the midline of the toe, the area equivalent to the scansorial cleft in *Bavayia*. Adipose cells also fill the posterior portion of the pad in *Rhacodactylus*. In *Rhacodactylus*, however, adipose tissue has not been associated with regions dorsal to the scansors in the lateral regions of the pad. The fat channel in *Rhacodactylus* appears to be a semi-controllable mechanism for the conformation of the pad to the substrate in the midline. The combination of vascular and adipose tissue as a means of control and/or mechanism of conformity of the scansors thus appears to be a general feature of the New Caledonian carphodactylines (it may be independently derived in *Bavayia* and *Rhacodactylus*, or lost in *Eurydactylodes*). The combination of the two systems (vascular and adipose) deep to the scansors of *Rhacodactylus*

may be a solution to the problem of support in extremely wide (in both relative and absolute terms) digits. The problem of support in the much smaller digits of *Bavayia* and *Eurydactylodes* has been solved in different ways.

In *Eurydactylodes* the digits, though wide relative to the animal's size, are tiny in absolute terms. Here the sinus is so large in relation to the pad that it is able to provide active control of the scansors in the absence of adipose deposits. The less arcuate penultimate phalanx of this taxon retains the ability to efficiently transduce forces onto a single, central vascular sinus (see Fig. 10A) which regulates pressure throughout the scansors by way of a reticular vascular network.

In *Bavayia* pad control is achieved by pad division and concomitant vascular modification (Fig. 10B). The high arch of the penultimate phalanx probably precludes the direct use of a central adipose core as seen in *Rhacodactylus*, and the median scansors are lost in favour of the dual scansor control mechanism. With the divisions of the subdigital plates and the elevated penultimate phalanx comes the requirement for lateral support of the pad, as the control mechanisms become at least partly restricted to one side of the digit or the other. Among divided-scansored gekkonines the position dorsal to the divided sinuses may be filled with adipose tissue, as in *Thecadactylus* or with incipient paraphalanges, as in *Homopholis* (Russell and Bauer, 1988). Clearly, a number of solutions to the problem of transducing pressure onto the lateral scansors are possible. *Bavayia*, starting with a diplodactyline or, more specifically, a carphodactyline heritage (and its concomitant constraints) has solved the problem by maintaining a partially undivided sinus (thus allowing some central transduction of force from the penultimate phalanx) and by utilising a dorsal adipose zone to distribute pressure laterally. Basally in the digits, proximal to the scansors, extensive fat deposits are also present (Fig. 9) and *Bavayia* thus maintains at least some passive control of the mechanism of substrate conformation in the series of friction plates.

FUNCTION

There is little information available about the biology of New Caledonian geckos, especially those of the genus *Eurydactylodes*. As far as is known, both *Eurydactylodes* species are exclusively arboreal (Roux, 1913; Meier, 1979) and seem to prefer branches of small diameter. *Bavayia cyclura* dwells primarily on trees or in

FIG. 8. Cross-section through the proximal portion of digit IV, right pes of *Bavayia sauvagii* (author's collection, AMB 267) showing the adipose zone (AZ) beneath the phalanx and above the friction plates (FP). Adipose invested connective tissue also fills much of the remainder of the digit. Scale bar = 250μm.

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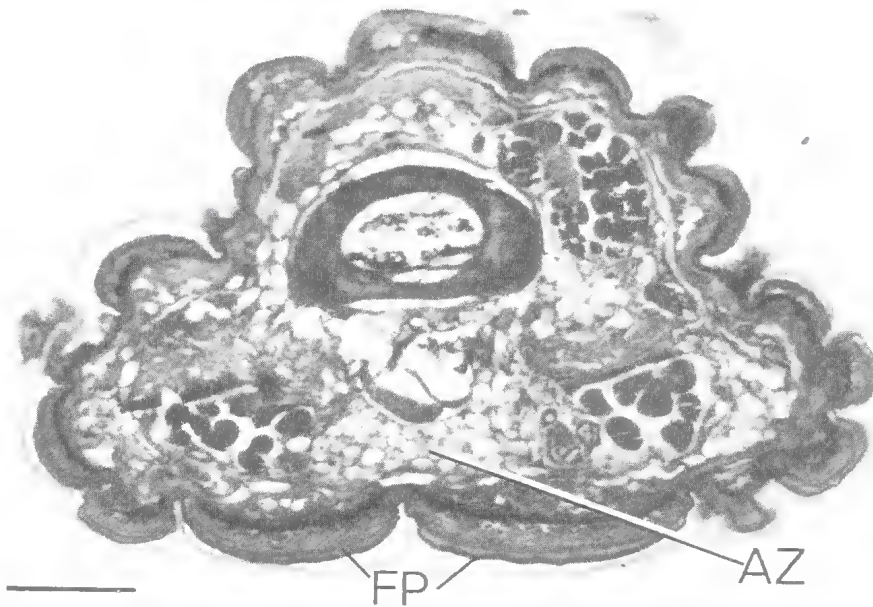


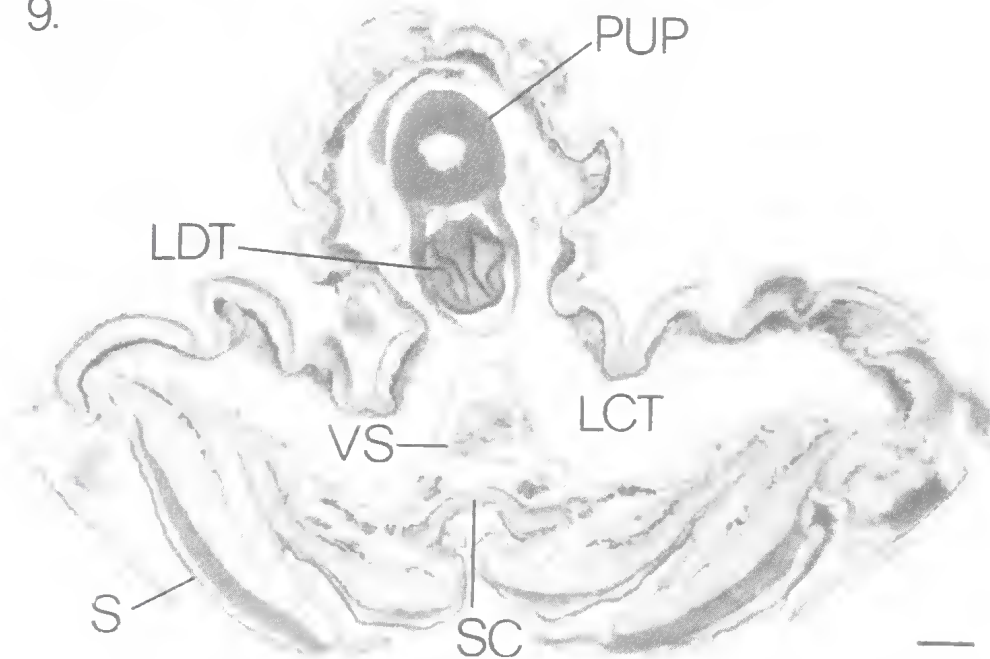9.



FIG. 9. Cross-section through digit IV, right pes of *Bavayia sauvagii* (AMB 506) at the level of the penultimate phalanx. Note the division of the vascular sinus into two lateral branches on either side of the scansor cleft (SC) and the presence of loose connective tissue (LCT) containing adipose deposits above the branches of the sinus. Other abbreviations as in Figure 5. Scale bar = 250μm.
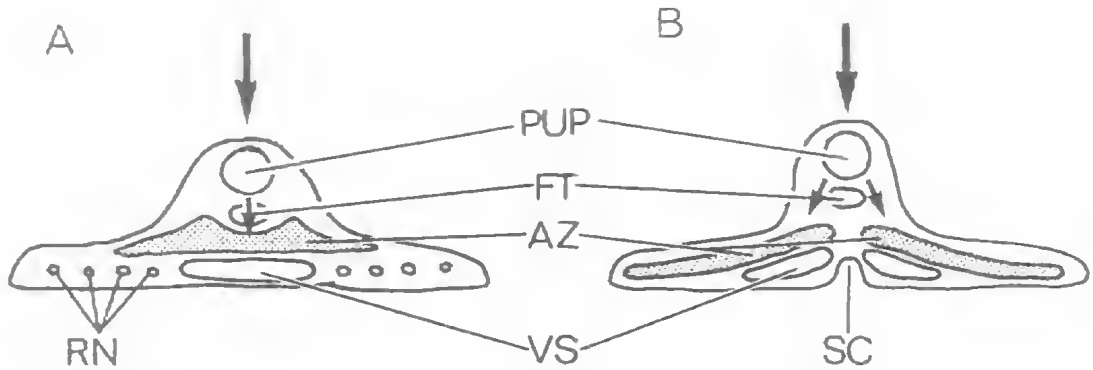
FIG. 10. Diagrammatic sections through the distal portions of the digits of A. *Rhacodactylus/Eurydactylodes* (adipose zone would be lacking in the latter) type toe and B. *Bavayia* type toe. In A forces are transduced directly to the sinus or through the adipose zone to the sinus through the midline of the toe. An extensive reticular network of blood vessels (RN) is present. In B some transduction of pressure is direct while the remainder is spread through the adipose zone. FT = flexor tendon. Other abbreviations as in previous figures.

logs and stumps (Roux, 1913; Meier, 1979; Bauer, 1986). *Bavayia sauvagii*, although generally perceived as arboreal, spends much of its time under rocks in terrestrial microhabitats, although animals may also live in tree holes or climb saplings at night to feed (Bauer and De-Vaney, 1987). Unfortunately our knowledge of the pedal performance requirements of scansors on different substrates is rudimentary. Further, the relative importance of claws versus scansors on substrates such as wood is unknown. Indeed, factors of safety (sensu Alexander, 1981) in digital design (with respect to both claws and scansors) appear to vary greatly among even closely related geckos (Bauer and Good, 1986) and parts of the scansorial apparatus may be 'overdesigned' by more than an order of magnitude.

Despite our ignorance, however, it is probable that divided scansors as seen in *Bavayia* do offer some advantage in terms of control. By possessing independently functioning halves of each subdigital plate, the animal is able to exert finer tendinous and vascular control over the scansor and the scansor pairs themselves are freer to deform to substrate irregularities. None the less, finer control of the scansors is also associated with a less direct transduction of forces onto the blood sinus and the 'advantage' (if any) of the divided scansor design of *Bavayia* over the single scansor of *Eurydactylodes* or *Rhacodactylus* is difficult to determine. The only valid assessment of the efficiency of these alternative designs would be one which was based upon performance of the morphologies in direct com-

petition. Although many alternative solutions may suffice for a given problem of locomotor performance, some may be more effective than others under competitive circumstances (Russell, 1976). Such situations are rare in nature but the exclusion of certain native geckos from human-commensal habitats by the introduced divided-scansored gekkonine *Hemidactylus frenatus* in both Hawaii (Hunsaker and Breese, 1967; McKeown, 1978) and New Caledonia (Bauer and Vindum, unpublished) may be indicative of the advantages of a particular digital design under certain circumstances. No such head-to-head competition appears to occur between *Bavayia* and *Eurydactylodes* but it may be valid to evaluate the relative 'success' of the two forms by means of their geographic distribution and abundance. The species of *Bavayia* (actually species complexes, Ross Sadlier, pers. comm.) are distributed across all of New Caledonia and the Loyalty Islands and occupy habitats from houses and beach wrack to rainforest and savanna, from sea level to over 1000m (Bauer, 1986). In contrast, the species of *Eurydactylodes* are known from scattered localities on the New Caledonian mainland and may be limited to regions of the edaphic vegetation of lateritic soils (Bauer, 1986; Bauer and Vindum, unpublished). Likewise, *Bavayia* is generally encountered in large numbers in the field, while *Eurydactylodes* is rarely found and has never been reported in high densities. Of course the patterns of species density and distribution are more than simple reflections of digital design. All other attributes of the animals' biology, as well as the com-

plexity of habitat type, and the vagaries of the search images of human collectors all combine to yield these patterns. None the less, the divided scansors of *Bavayia* may have played a role in the spread and habitat diversification of the genus.

For the time being it seems prudent to regard the differences observed between *Bavayia* and *Eurydactylodes* as merely alternative designs for arboreal or semi-arboreal pedal function rather than specific adaptations for particular microhabitats or surface features. It is clear that both morphologies suffice for their possessors and it is likely that many other designs could also perform effectively in the same habitats. Optimality may be a useful concept in theoretical considerations of biological phenomena but to our knowledge, animal morphologies are not, nor should they be expected to be, optimally constructed. Adaptation of the organism to its environment at this level is trivial (see Gould and Lewontin, 1979). The most (or only?) valid assessment of the 'adaptation' of alternative scansor designs is that which incorporates both biotic and abiotic features of the environment into the determination of selective value. Unfortunately, in the study of gekkonid morphology we are only at the stage that we can identify differences and suggest reasons (phylogenetic, functional, structural or stochastic) for their existence. A complete analysis of the 'meaning' of alternative scansor design in *Bavayia* and *Eurydactylodes* must await a more detailed and fine-grained understanding of the biology of these taxa.

## ACKNOWLEDGEMENTS

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